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Shortage in available N is the main nutrient factor limiting the growth of forest. As acid precipitation involves increased deposition of N in available forms, increased tree growth is likely. In soils with low SO_4 adsorption capacity, which probably cover much of the boreal zone, acid precipitation also involves increased leaching of Ca, Mg and possibly K. Together with the possible increase in tree growth, this might enforce deficiencies in these elements in the future.

Introduction

The pollution of the atmosphere has involved increased deposition of H^+ , S, and N. Other elements, and in particular heavy metals, are also deposited in higher amounts than before. However, only the effects of H^+ , S, and N will be considered in the present paper.

The deposition of SO_4^{2-} in Europe has increased 2–3 % per year during the last 20 years, while the NO_3^- deposition has increased about 5 %.¹ Today the deposition of H^+ from precipitation over large areas of Europe and North America is between 0.1 and 1 kg ha^{-1} year⁻¹.^{1,2} The wet deposition of excess SO_4^{2-} in Europe appears to be on the order of 5–25 kg S ha^{-1} year⁻¹. The total deposition, both dry and wet, is on the order of 10–120 kg S ha^{-1} . The deposition of N has not been studied in the OECD programme on long range transport of air pollutants. However, estimates from Norwegian data indicate a wet deposition on the order of 2–14 kg N ha^{-1} year⁻¹.^{3,4} Deposited N is composed equally of NO_3^- and NH_4^+ . The dry deposition of N is incompletely known. However, estimates of the ratio of dry deposition to wet deposition of NO_3^- appear to vary from about 5 in areas close to the emission sources to about 1 in areas remote from sources (300–3000 km).⁵ In a rural area in southern Sweden the wet deposition of N was estimated to be about 5.6 kg ha^{-1} year⁻¹, whereas the dry deposition amounted to about 8 kg ha^{-1} .⁶

The present paper deals with the effect of acid precipitation in areas remote from emission points. In such areas visible injury to vegetation has not been reported, and the SO_2 concentrations are generally much lower than those producing injury to plants. Acid precipitation in these areas therefore appears mainly to be a problem concerning the nutrition of forest trees.

Nutrient requirement of forest trees

Green plants build up their tissue from elements taken out of air and soil. In addition to the main structural elements of plant tissue, C, O, and H, the essential elements for plants are N, P, S, K, Ca, and Mg. The other elements also required, but in very small amounts, are Fe, Mn, Cu, Zn, B, Mo, Cl, and for some plant species also other elements.

The different plant species do not require equal amounts of nutrients, nor in equal proportions. One of the basic principles, however, is that plant growth is regulated by the factor(s) in minimum. This principle was formulated by the German investigator C.S. Sprengel and called the law of minimum. This law is still in force, but it is important to realise that plant

production can be stimulated by several factors simultaneously and that increased growth depends on interactions between these factors.

The nutrient requirement of a plant also depends on its stage of development. In connection with production of seedlings of forest trees, studies on their nutrient requirements have been carried out in solution cultures.⁷ On the basis of these studies optimum foliar concentrations for plant growth and concentrations corresponding to visual deficiency symptoms in Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birch (*Betula verrucosa*) have been found. Table 1 shows the concentrations giving visual deficiency symptoms in these species. Measured as dry weight percentage, the amounts of S, P, Mg, and Ca causing deficiency symptoms in the foliage vary between 0.02 and 0.21 %. Even though K is not used as a constituent of organic compounds in the plants, the requirement of this element appears to be much higher than for S, P, Mg, and Ca. Disregarding the structural elements C, O, and H, N is the element needed in highest amounts by plants. The lower limit for deficiency in N appears to be between 0.7 and 3.1 %. Calculating the concentrations as mol kg^{-1} and comparing the requirements for N, K, P, S, and Mg to that for Ca, it is found that the species need approximately 35–240 times more N, 4–15 times more K, and 1–8 times more S, P, and Mg than Ca.

Table 1. Macronutrient concentrations corresponding to visual deficiency symptoms in forest trees⁸

	Percentage of dry weight		
	Pinus	Picea	Betula
N	0.7 – 1.6	1.0 – 1.7	1.5 – 3.1
K	0.3	0.3	0.5
S	0.07	0.13	0.06– 0.21
P	0.06–0.09	0.05–0.11	0.12
Mg	0.06	0.02–0.07	0.06–0.18
Ca	0.05	0.02	0.12

In order to optimize growth the different nutrients must be given in proper proportions. N and S are for example needed in proportions reflecting approximately the composition of plant proteins, which corresponds to a N/S mol ratio slightly larger than 30. It is also important to know that high uptake of one element might affect the uptake of other elements. High amounts of K might thus inhibit the uptake of Mg. High amounts of Al in agricultural soils influence the uptake of other cations and P. Forest trees, on the other hand, appear to be much less sensitive to high Al concentrations.^{8,9} Also the form in which the nutrients are given is important. If N is given as NO_3^- to a calcifuge species grown at high soil pH, toxic levels of Ca might be found in the plant tissue.¹⁰

Even under laboratory conditions and solution cultures, plant nutrition is complicated, and complex interactions with growth factors other than the nutrients also exist. Under natural conditions this problem is even more complex. Knowledge

of the nutrient requirement of natural forest is therefore limited. Most of the knowledge is based on fertilizer experiments.

The main element limiting the growth of forest trees under natural conditions is N.^{11, 12, 13, 14, 15, 16} N fertilization is therefore a widely used method for increasing forest production. For example, in Scandinavia about 200 kg of N ha⁻¹, mostly in the form of NH₄NO₃ or urea, often is applied 5 to 10 years prior to the final cutting. Trials with N fertilization often give highly variable results. Recently it has been reported that the lack of response to N fertilization in some cases might be caused by an insufficient supply of S.^{17, 18, 19} These findings appear to demonstrate that with a low SO₄²⁻ content in the needles, an increased supply of N can not be utilized because of insufficient amounts of S for the synthesis of proteins. On the other hand, when SO₄²⁻ is abundant in the foliage, an increased N supply can be utilized. The results also demonstrate that analysis of foliage SO₄²⁻ might be a valuable diagnostic method for predicting the response to N fertilization. It seems likely that similar relationships also exist between N and other nutrient elements, and that this might explain some of the varying responses to N fertilization.

Pure S deficiency has only been reported from restricted areas in the temperate zone. In areas with mature soils however, as in the tropics and areas in the temperate zone not glaciated, S deficiency appears to be more common.^{20, 21}

Also the other main nutrient elements have been reported to be limiting for the growth of forest trees. Deficiencies of these elements are much less widespread than N deficiency. P and K deficiencies are, however, very common in plantations on drained peatland. K and Mg deficiencies are reported from a number of European and North American mineral soils.²⁰ It is otherwise important to realize that fertilization with one element, or other incomplete fertilizers, is likely to bring about deficiencies in other elements.

Effects of acid precipitation on the amount of plant nutrients in forest ecosystems

When evaluating the effect of acid precipitation on the supply of plant nutrients in a forest, a basis could be to consider the nutrient cycle in a terrestrial ecosystem (Fig. 1). Plant available nutrients are generally supplied to the system from two sources; from the atmosphere, as for N and S, and from the minerals, as for Ca, Mg, P, K, S, and the micronutrients. In natural systems not harvested by man, nutrients are also lost in two ways: to the atmosphere by volatilization and to the sea by leaching. Evaluation of the effect of acid precipitation on the amount of plant nutrients in a forest ecosystem can therefore be restricted to consideration for four processes: deposition from the atmosphere, weathering, volatilization and leaching from the soil. Obviously many processes in the soil and the plants can affect the accessibility of plant nutrients. Acid rain may affect some of these processes. These problems, however, are the subjects of other contributions to this conference.

Knowledge of the influence of increased deposition of H⁺, S, and N on leaching of plant nutrients can be gained from a number of watershed and lysimeter studies in North America and Europe.^{22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32} Figure 2 shows the relationship observed in these studies between the input of N by precipitation versus the output. It appears that the leaching of N in general is much smaller than the input by precipitation. In fact the output by streams or by leaching is on the average only 30% of the input by precipitation. This means that approximately 70% of the input by precipitation appears to be retained in the system. N is also deposited in the system as gases and particles. The dry deposition may be of the same order of magnitude as the wet deposition.^{1, 6, 7} In the Hubbard

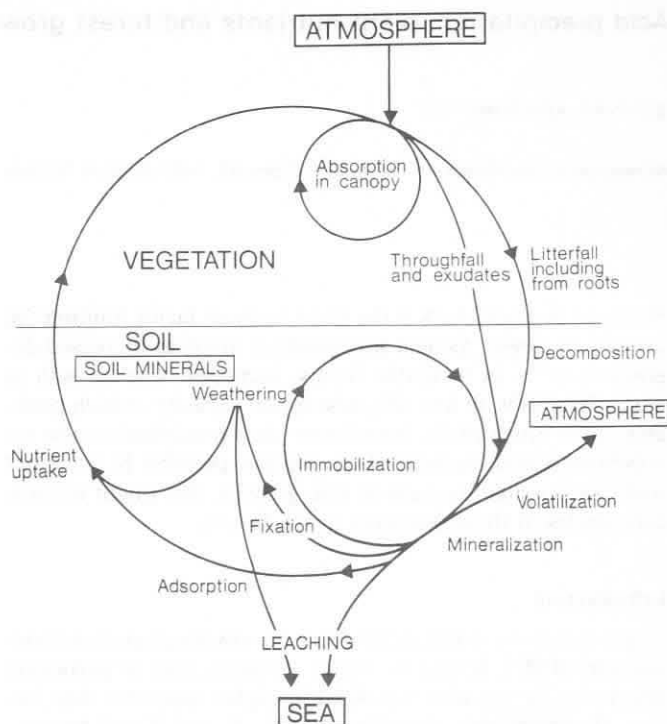


Figure 1. Simplified diagram of the nutrient cycling in terrestrial ecosystems.

Brook experimental forest estimates of input of N by precipitation (6.5 kg ha⁻¹), loss of N in the stream, and accumulation of N in the forest biomass, indicate that approximately 14 kg of N ha⁻¹ year⁻¹ must enter the ecosystem in a gaseous form of from impacted nitrogenous aerosols.²² Some of this input is due to deposition of air pollutants, the remainder to natural processes. In Sollingen the input of N by precipitation has been estimated at 23 kg ha⁻¹ year⁻¹ whereas about 6 kg entered the system by canopy filtering.²⁹

Figure 2 does not indicate that the relative loss of N increases with increasing N input. Increased deposition of N is correlated to increased acidity of precipitation. Therefore, the figure does not indicate that the relative loss of N increases with increasing acidity of the precipitation. As nitrification generally is inhibited by soil acidification, and as NO₃⁻ is more readily leached from the soil than NH₄⁺, one would expect reduced leaching of inorganic N with increasing soil acidity. Ly-

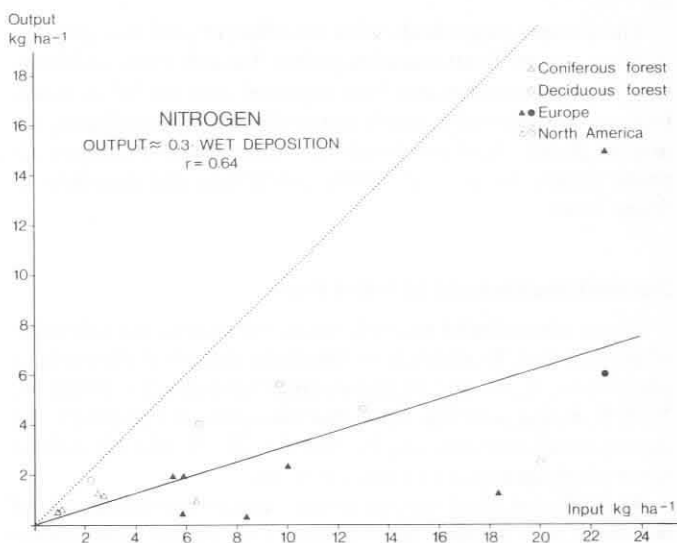


Figure 2. Annual input of (NH₄⁺ + NO₃⁻) - N by precipitation versus the leaching losses from forest watersheds and lysimeters with forest soils. Solid line is the regression line, dotted line is the 1:1 line. Data from studies in Europe and North America - see text for references.

simeter experiments carried out with artificial acid rain have not revealed any significant effect on the leaching of N when the acidity of the rain varied between 6 and 3.^{32, 33, 34} However, the most severe acidification in these experiments (pH 2.5 – pH 2) brought about a significant leaching of both NH_4^+ and NO_3^- . This effect probably has little relevance to the acid rain problem with the present concentrations of strong acids. It may have been caused by reduced competition for N in the soil as the treatment has damaged part of the forest floor vegetation. As heterotrophic nitrification has been suggested to occur in acid soils this possibility can not be excluded.³⁵

The studies referred to indicate that substantial amounts of N might be accumulated in terrestrial ecosystems exposed to acid precipitation. This, however, is based on the assumption that the amount of N volatilized is negligible. To my knowledge no studies have been carried out that can be used to quantify the possible gaseous losses. There are, however, contributions to this conference that deal with the stability of NO_2 in acid conditions.

The output of S from the watersheds and lysimeters is much larger than the output of N (Fig. 3). In general the output of S is also greater than the input by wet deposition. Including the dry deposition, which may vary from less than 25% in areas remote from emission points to 4–8 times the wet deposition in areas close to the emissions,^{1, 5} the average output of S by leaching may be slightly smaller than the total deposition. As for N, the gaseous loss of S can not be quantified. However, assuming some volatilization one might conclude that in the northern part of the temperate zone there appears to be an approximate balance between the input and output of S.

The greater leaching of S compared to N might be surprising as it is known that SO_4^{2-} can be more strongly adsorbed to soil particles than NO_3^- . The explanation apparently is that NO_3^- is tied up in the cycle between vegetation and soil, and as long as N is a limiting element, leaching losses will be small. S, on the other hand, is usually not a limiting element and leaching loss is possible. The adsorption of SO_4^{2-} in soils is the subject of other contributions to this conference. Nevertheless it should be mentioned that SO_4^{2-} adsorption appears to be much greater in mature soils than in young soils (see the tropical site in Fig. 3). This is due to the higher sesquioxide content in old soils.^{36, 37, 38, 39}

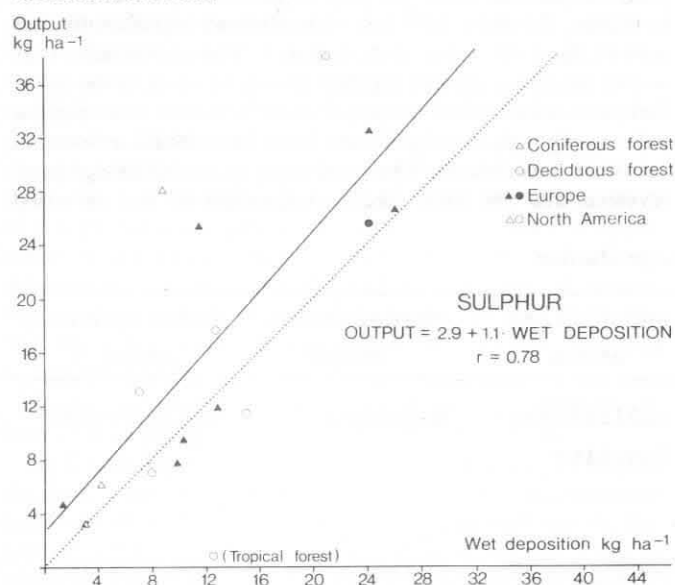


Figure 3. Annual input of SO_4^{2-} - S by precipitation versus the leaching losses from forest watersheds and lysimeters with forest soils. Solid line is the regression line, dotted line is the 1:1 line. References as for Fig. 2.

K, Mg, Ca, and perhaps P are mostly leached in much higher amounts than the input from the atmosphere.^{22, 23, 25, 27, 28, 33, 40, 41} The difference between atmospheric input and output by streams gives an estimate of the weathering in natural ecosystems. In the Hubbard Brook forest ecosystem weathering has been estimated to mobilize about $2 \text{ ke ha}^{-1} \text{ year}^{-1}$ of cations. This amounts to about 20 kg ha^{-1} of Ca, 6 kg ha^{-1} of Na, 3.5 kg ha^{-1} of Mg, 7 kg ha^{-1} of K, 2 kg ha^{-1} Al, and 18 kg ha^{-1} of Si.²² In the valley of Numedal in Norway weathering has been estimated at $1 \text{ ke ha}^{-1} \text{ year}^{-1}$.⁴²

The influences on the leaching of K, Ca, and Mg are among the most discussed effects of acid precipitation. By ion exchange reactions between H^+ and metal cations and by increased SO_4^{2-} leaching, a net increase in the leaching of K, Mg

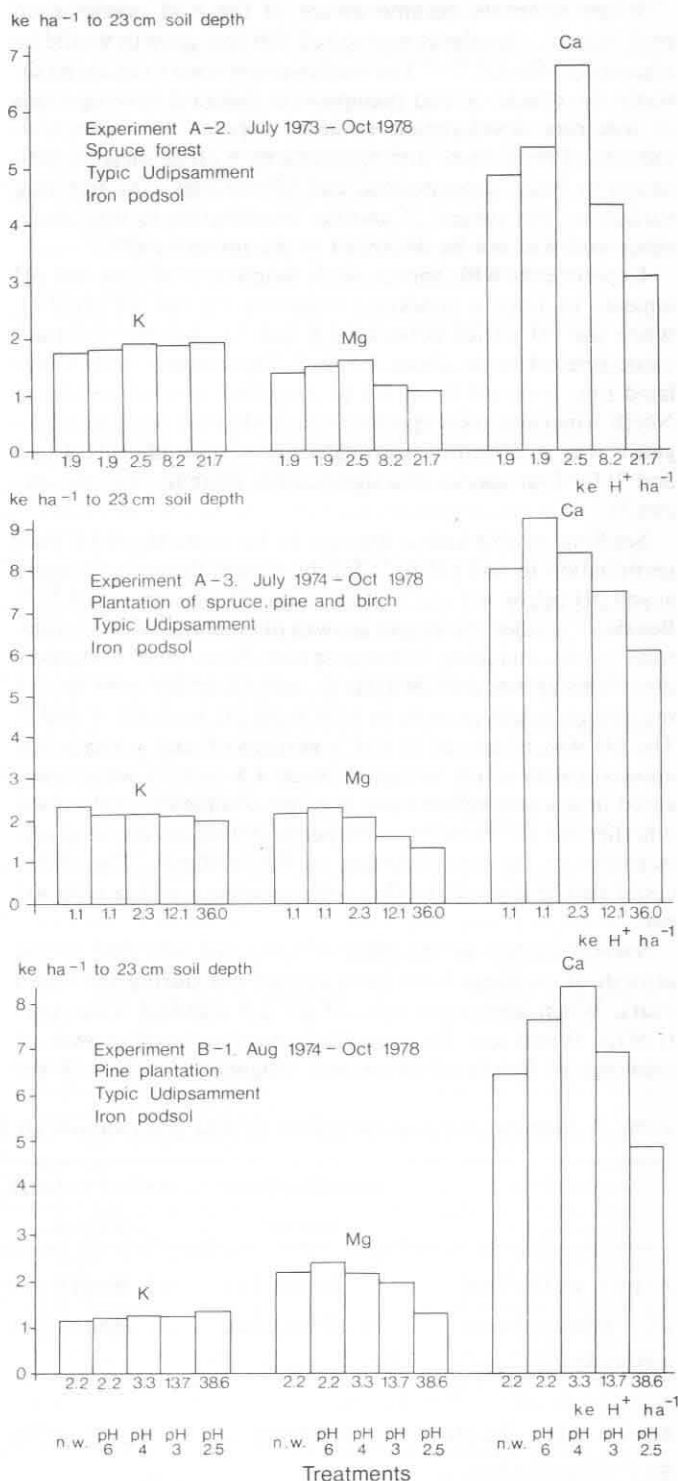


Figure 4. Effects of the acidity of artificial rain on the total amount of extractable K, Mg, Ca in the upper 23 cm soil layer. Data from Norwegian experiments on iron podsoles or Typical Udipsammets.

and Ca is likely. This has also been shown experimentally.^{32, 33, 34, 43} The increase in leaching by increased acidity of artificial rain is most significant for Ca and Mg; K appears to be less sensitive. Acid precipitation will most likely increase the weathering rates in the soil. The crucial point therefore is if the increase in weathering can compensate for the increased leaching losses. Experiments with artificial acidification have shown that increased application of acid to soils appears to increase the leaching more than the weathering. The result therefore appears to be a reduction in the pool of exchangeable Ca, Mg and Mn in the soil (Fig. 4).^{32, 33, 34, 44} K appears to be less influenced by the acidification.

Effects of acid precipitation on tree growth

When scientists became aware of the acid precipitation problem, the hypothesis was raised that tree growth would be negatively affected.^{45, 46} The studies established to examine directly the effects of acid precipitation included investigations of tree ring development in areas exposed to different amounts of deposition, and experiments with artificial acidification in fields, greenhouses, and laboratories. The tree ring studies are the subject of another contribution to this conference and will not be discussed in the present paper.

Experiments with spruce seeds demonstrated that soil pH appears to have a moderate influence on the germination when the pH varied between 3.8 and 5.6, but the optimum value seemed to be about 4.7.^{33, 47} Experiments with simulated rain with pH from 5.6 to 3 applied to seeds of eleven North American trees species showed that the seedling emergence was significantly stimulated by acid «rain» (pH 4, 3.5 and 3) for four species and significantly inhibited for one species.⁴⁸

Seedling establishment appears to be more sensitive than germination to soil pH.^{33, 48} Establishment decreased rapidly at soil pH below 4.4 and the optimum pH was about 4.7.^{33, 47} Benizian⁴⁹ studied the height growth of seedlings of ten coniferous species including Norway spruce, Scots pine, Lodgepole pine, Sitka spruce and Douglas fir, and found for most species maximum height growth in soils with pH between 4 and 5. The pH was measured in CaCl_2 suspension and corresponds approximately to pH values between 4.5 and 5.5 when measured in a water suspension. It is not completely understood whether the H^+ concentration per se influences the seed germination or the establishment of the seedlings. The effects could also be caused by other soil properties varying with soil pH.

Several studies on the effect of simulated acid rain on the growth of seedlings have been carried out during the last 6 years. When applying a mist of pH 2.3 (distilled water plus H_2SO_4), Wood and Bormann⁵⁰ observed reduced growth of seedlings of *Betula alleghaniensis*. Higher pH values of the

mist did not significantly affect the growth. Matziris and Nakos⁵¹ worked with *Pinus halepensis*, which according to Benizian⁴⁹ appears to be a species preferring less acid soils than most conifers. They found reduced seedling growth by application of distilled water acidified with H_2SO_4 to pH 3.1 and 3.5, compared to non-acidified water.

The other experiments with seedlings have shown no effect of the acidity of the simulated rain or increased growth by some of the acid treatments. Wood and Bormann⁵² found increasing growth with decreasing pH of their simulated rain, the acidity of which was adjusted by H_2SO_4 , HNO_3 , and HCl in the proportions of chemical equivalents, SO_4^{2-} 66%, NO_3^- 24% and Cl^- 10%. Lee and Weber,⁴⁸ using simulated rain acidified by H_2SO_4 , found increased seedling growth in the acid treatments compared to the control for Douglas fir and three North American deciduous species. As the soil used had a strong SO_4^{2-} adsorption property, they suggested that the concentration of SO_4^{2-} in the soil solution was low and that the growth effect was due to a fertilization effect of S taken up through the foliage. Ogner and Teigen⁵³ applied simulated rain of pH 5.4, 4, 3, and 2.5 to rooted cuttings of two clones of Norway spruce. They found a slight increase in dry matter production with increasing acidity of the rain. The increase was, however, not statistically significant. In another study they applied rain of pH 5.4 and 2.5 to cuttings of seven clones of Norway spruce grown at three different temperatures.⁵⁴ In this case they found a highly significant increase in growth by the acid treatment. The growth effect appeared to be caused by increased N uptake indicating increased mineralization of N in the soil.

Experiments on the effect of artificial acidification on forest growth under field conditions have been carried out in Sweden and Norway. The Swedish experiments have shown that increasing application of dilute H_2SO_4 has significantly increased the basal area growth.⁵⁵ The experiment also includes N fertilized plots. Application of 720 kg of N ha^{-1} over a nine-year period increased the basal area growth about 40%. In the fertilized plots application of acid significantly reduced the growth. The Norwegian studies consist of five field plot experiments where artificial rain has been produced by mixing groundwater and H_2SO_4 to pH values from 6 to 2.^{32, 33, 56} In one experiment with Scots pine increased height and diameter growth was observed in 1976 and 1977 at the plots supplied with 250 mm of water per year of pH 3, 2.5 and 2. In 1979 however, the most acidified plots showed significantly less growth than the other experiments.⁵⁷ The experiment thus shows increased growth the first couple of years in the acidified plots, followed by decreased growth the last year. Similar patterns, though not significant, have been found in some of the other experiments. Chemical analyses of the foliage have revealed that the most likely explanation of the increased

Table 2. Summary of possible effects of acid precipitation on forest production.

	N-deficient areas	S-deficient areas	K-deficient areas	Mg-deficient areas	P-deficient areas
Areas with low SO_4 adsorption capacity	1. Positive 2. Negative	1. Positive 2. Negative	Indifferent- Negative	Negative	Indifferent?
Areas with high SO_4 adsorption capacity	Positive	Positive	Indifferent	Indifferent	Indifferent

1. Short term effects

2. Long term effects

growth is increased N uptake. The increased growth can not be related to increased S uptake as found by the foliar analyses. The decrease in growth observed in 1979 might be related to reduced availability of Mg as the foliar concentration is close to values giving visual deficiency symptoms.⁵⁷

Conclusion and summary

Apart from possible direct effects of acid precipitation on forest trees, the effects on forest growth can be considered as a nutrition problem. The increased deposition of N and S can be regarded as an eutrophication or fertilization effect, and the increased leaching of nutrient cations caused by the increased leaching of SO_4^{2-} can be regarded as an oligotrophication or acidification effect. Experience from forest fertilization is therefore useful when evaluating the effects of acid precipitation on forest growth. The fertilizer experiments in temperate forest have shown that N, K, P, Mg, and S individually or in combinations might restrict growth of forest trees. The requirement of forest trees for micronutrients is incompletely known, but deficiencies of these nutrients also occur. These factors alone indicate that a generalization of a common effect of acid precipitation for most forest is impossible. In addition the influence of acid precipitation on the loss of plant nutrients by leaching is highly dependent on soil properties.

This, however, does not mean that we are unable to make some generalizations. The theory of the effect of the mobile anions on the leaching of plant nutrients from soils involves that the effects in areas with high SO_4^{2-} adsorption capacity will be different from those in areas where the adsorption capacity is low (Tab. 2). The SO_4^{2-} adsorption capacity is related to the amount of Al and Fe oxides in the soil. The sesquioxides are enriched during soil formation processes. Therefore, young soils developed after the last glaciations, generally have less anion adsorption capacity than soils developed during a longer period. In areas with high SO_4^{2-} adsorption capacity, effects of acid precipitation on tree growth would be expected to be positive in areas where N and/or S are growth limiting elements. In areas where other macronutrients are deficient, acid precipitation probably will not significantly influence the growth. In areas with low SO_4^{2-} adsorption capacity, which probably include large areas of the boreal forest, the main growth limiting element is N. Experiments with artificial acidification in these areas have shown that the availability of N in the soil for some reason or other might be increased. This, however, appears to be a temporary effect caused by extreme acidification. Therefore, little importance should be attached to this effect. More important is the increased deposition of inorganic N from the atmosphere, which most likely will increase the tree growth. The long term effect of the deposition of N is probably comparable to the long term effects of application of incomplete fertilizers. This most likely will enforce deficiencies in other elements, preferably K, Mg, P and/or some micronutrients. For some elements, and in particular Mg, this effect might be strengthened by increased leaching caused by acid precipitation.

Similar arguments can be applied when evaluating the effects of acid precipitation in sulphur deficient areas.

In K and Mg deficient areas acid precipitation is likely to strengthen the nutrient deficiencies. However, experiments have shown that the effect of acidity of artificial rain on the leaching of K is less than on Mg. Therefore, the tree growth might be more negatively influenced by acid rain in Mg deficient areas than in K deficient areas. It is, however, also possible that when a nutrient is in minimum the nutrient cycle becomes tighter and leaching losses due to acid precipitation might be small.

The discussion shows that the previous general hypothesis that acid precipitation significantly will decrease forest production over large areas must be revalued. The deposition of N and to some extent S (tropical and subtropical areas) is likely to increase forest production. Reduced growth may be expected where or when nutrients like Mg and possibly K are the growth limiting elements.

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